STATISTICAL REPORTS

SEASONAL COMPONENTS OF AVIAN POPULATION CHANGE: JOINT ANALYSIS OF TWO LARGE-SCALE MONITORING PROGRAMS

WILLIAM A. LINK[1] AND JOHN R. SAUER

USGS Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA

Abstract. We present a combined analysis of data from two large-scale surveys of bird populations. The North American Breeding Bird Survey is conducted each summer; the Christmas Bird Count is conducted in early winter. The temporal staggering of these surveys allows investigation of seasonal components of population change, which we illustrate with an examination of the effects of severe winters on the Carolina Wren (*Thryothorus ludovicianus*). Our analysis uses a hierarchical log-linear model with controls for survey-specific sampling covariates. Temporal change in population size is modeled seasonally, with covariates for winter severity. Overall, the winter–spring seasons are associated with 82% of the total population variation for Carolina Wrens, and an additional day of snow cover during winter–spring is associated with an incremental decline of 1.1% of the population.

Key words: Breeding Bird Survey; Carolina Wren; Christmas Bird Count; hierarchical models; seasonal population change; snow cover; Thryothorus ludovicianus; *winter weather effects.*

INTRODUCTION

Time series of counts, such as those obtained from the continent-scale North American Breeding Bird Survey (BBS; Robbins et al. 1986) and Christmas Bird Count (CBC; Bock and Root 1981) are a primary source of population information on most North American bird species and are used in a variety of conservation and research activities (e.g., Sauer et al. 2003, Thogmartin et al. 2004). Understanding the consequences of exogenous events such as severe winters is fundamental to population modeling and management. For example, one prediction of climate change modeling is that the frequency of these extreme weather events should increase (Root and Schneider 1993); a need exists to better document seasonal effects of weather on bird populations (Robbins et al. 1986). Clearly, rates of change estimated from annual counts cannot be unequivocally associated with specific demographic events, which occur at relatively short temporal scales within the yearly cycle. However, surveys do occur at different times of year, and aggregation of information among surveys can be used to estimate seasonal patterns of population change.

In this paper, we describe a joint analysis of data from the BBS and CBC. These surveys are conducted

annually: the BBS in June and the CBC in December. Our goal is to exploit the temporal staggering of the two surveys in order to estimate seasonal components of population variation not identifiable from either survey, taken alone. We designate the period from December to June as "winter–spring" (W–S) and from June to December as "summer–fall" (S–F). For nonmigratory bird species, seasonal components of variation are entirely associated with rates of population change. In particular, the W–S component of population change is entirely associated with winter mortality (young of the year are excluded from BBS counts). Our presentation does not address the application of these models to migratory species, for which the seasonal components of population change would include movement rates.

We investigate the effect of severe winters on survival of Carolina Wrens (*Thryothorus ludovicianus*). Carolina Wren populations exhibit rapid growth punctuated by precipitous declines (Fig. 1), which have been associated with severe winters (Sauer et al. 1996). The Carolina Wren is nonmigratory (Bent 1966). Because it is a ground-foraging species, extended periods of snow cover cause starvation; birds that survive the winter in northern regions are dependent on snow-free areas (Wetmore 1919, Bent 1966). Mehlman (1997) used interval-specific averages of counts on BBS routes to document the effects of winters in the 1970s on local Carolina Wren populations. He found that declines were associated with distance to edge of range, winter severity, and abundance. We estimate the proportion

of yearly variation associated with winter for the species, and extend Mehlman's (1997) investigation by modeling the effects of winter severity (as indexed by days of snow cover) on seasonal components of population change.

Combining information from multiple surveys is complicated by a fundamental limitation of most animal surveys: the data collected are not complete counts of populations; the surveys are not censuses. The widespread tendency to refer to surveys as censuses would be reasonably harmless, merely a matter of linguistic imprecision, were it not for a corresponding tendency to *conceive* of surveys as censuses, and to overlook sources of irrelevant variation in counts, variation that possibly may be confounded with population change. Legitimate analyses of count survey data are, of necessity, model-based, with controls for "detectability" being a crucial component (Link and Sauer 2002). Most model-based analyses control for detectability over time within surveys; few investigators have considered the possibility of between-survey modeling. However, hierarchical modeling methods provide new opportunities for development of realistic models for combining survey information, and Markov chain Monte Carlo methods provide a means of fitting complex hierarchical models. In this paper, we develop a hierarchical model for composite analysis of BBS and CBC data.

DATA SOURCES

The North American Breeding Bird Survey has been conducted every summer since 1966, with primary sampling units being 25-mile ($\sim$40.2-km) roadside routes. An individual observer is assigned to each route; the observer conducts three-minute counts at each of 50 stops along the route in accordance with protocols intended to reduce irrelevant sources of variation (Robbins et al. 1986). Nevertheless, there remains substantial variation in the number of birds counted by observers. Observers serve for a median of roughly three years, with $\sim$28% dropping out after only one year, and only 18% serving for more than 10 years. A general pattern of increasing counts has been noted among observers (Sauer et al. 1994); that is, new observers tend to count more birds, on average, over their years of service than did the observers that they replace. In addition, observers tend to count fewer birds than their average in their first year of service. Failure to account for these observer effects can be expected to lead to positive biases in estimation of population trends.

The Christmas Bird count has been conducted since 1900. Teams of observers are assigned to the primary sampling units, which are circles 15 miles ($\sim$24.1 km) in diameter (Bock and Root 1981). The CBC is primarily a recreational event, without formal attempts at standardization: team size and count duration vary widely. It has long been recognized that the amount of effort expended in producing CBC counts is an important explanatory variable for the counts, one with the potential of being
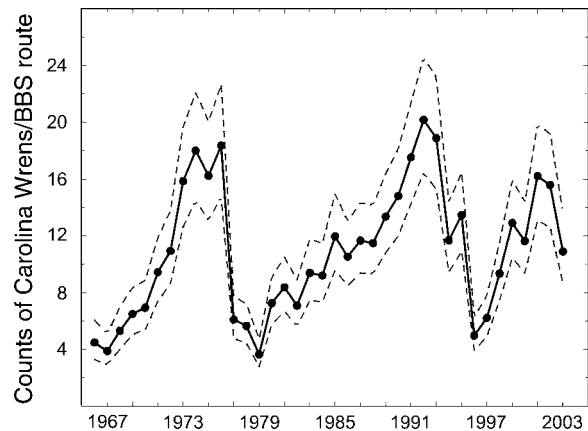

FIG. 1. Estimated population trajectory for Carolina Wren in the Maryland Coastal Plain, 1966–2003. The solid curve indicates the expected count by a typical BBS observer; dashed lines are 95% credible intervals.

confounded with patterns of population change (Butcher and McCulloch 1990, Link and Sauer 1999).

Thus for both data sources it is important to distinguish irrelevant sources of variation related to sampling from sources of variation related to population change. We do so in the context of a log-linear model, as now described.

MODEL

BBS data and CBC data are counts; hence they are naturally modeled as overdispersed Poisson random variables. We describe the dependence of a typical count C on explanatory variables using a log-linear model for λ, the conditional mean value of C. These models treat $\log(\lambda)$ as a linear combination of explanatory variables, namely,

$$\log(\lambda) = \text{sampling effects} + \text{population effects} + \text{noise}. \tag{1}$$

The data that we analyze come from 70 strata, intersections of states and physiographic regions described subsequently. All of the variables in our model are sub- or superscripted with indices: k, survey (CBC, BBS); y, year; s, stratum; and i, site within stratum. Denoting sampling effects by Ψ, population effects by μ, and noise by ε, we express our model more explicitly as

$$\log(\lambda_{y,s,i}^k) = \Psi_{y,s,i}^k + \mu_{y,s}^k + \varepsilon_{y,s,i}^k. \tag{2}$$

We begin with some general comments on model 2.

First, note that there is an independent value ε associated with each count. Poisson random variables have equal mean and variance, but count survey data typically have variance $>$ mean, even after having modeled effects of covariates; the noise ε is included in the model to account for such overdispersion. Values $\varepsilon_{y,s,i}^k$, are modeled as mean zero normal random variables, with survey-specific variance $\sigma_k^2(\text{Noise})$. Be-
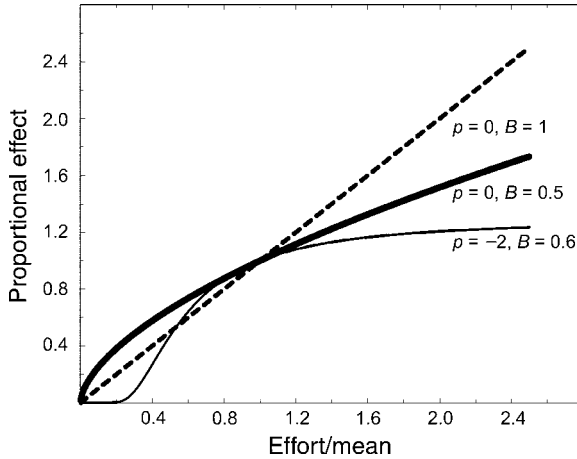
FIG. 2. Possible shapes of modeled effort effect $F(\xi) = \exp\{B[(\xi/\overline{\xi})^p - 1]/p\}$: $p \approx 0$, $B = 1$ (dashed line; counts proportional to effort); $p \approx 0$, $0 < B < 1$ (heavy solid line; diminishing returns, no asymptote); $p < 0$, $B > 0$ (light solid line; diminishing returns, asymptote). Here, B and p are estimable parameters controlling the relationship between counts and effort.

cause BBS data are being collected according to more rigorous protocols than CBC data, we anticipate that $\sigma^2_{\text{BBS}}(\text{Noise}) < \sigma^2_{\text{CBC}}(\text{Noise})$.

Next, note that the sampling effects Ψ are also specific to individual counts; these are modeled parametrically as departures from a baseline value of zero. Consequently, population effects $\mu^k_{y,s}$ correspond to typical counts for survey k, year y, in stratum s, adjusted for irrelevant sampling effects. There is no subscript i on $\mu^k_{y,s}$ in Eq. 2; we assume spatial homogeneity of population effects within strata. This homogeneity assumption, the nature of the sampling effects Ψ (to be described in more detail subsequently), and the availability of data from multiple sites within strata combine to render the population effects $\mu^k_{y,s}$ estimable.

Care must be taken to properly account for temporally varying sampling effects Ψ, or it will be impossible to use the count data for inference about population change. Such effects (e.g., effort for the CBC and observer effects for the BBS) are confounded with temporal change in population effects on counts, and the only solution is a model-based specification of Ψ. We present this first and then turn to modeling of population effects $\mu^k_{y,s}$.

Sampling effects

Sampling effects for BBS and CBC are modeled as parametric functions of covariates. These effects are not of primary interest per se, but must be included to avoid biases in estimation of the parameters of interest. For the BBS,

$$\Psi^{\text{BBS}}_{y,s,i} = \theta_{q(y,s,i)} + \eta F_{y,s,i}$$

where θ_q is the effect of observer q, F is an indicator of whether the count corresponds to the first year of service

of the observer, and η is the magnitude of the first-year effect. Note that observers are associated with a single BBS route, and that variation among θ_q reflects differences among routes within strata as well as variation among observers.

For the CBC,

$$\Psi^{\text{CBC}}_{y,s,i} = C_{s,i} + f(\xi_{y,s,i}).$$

Here, $C_{s,i}$ is the effect of circle i in stratum s, $\xi_{y,s,i}$ is the effort expended in producing the count, and $f(\xi)$ is a function describing the effect of effort on the proportion of birds counted. Specifically, we use

$$f(\xi) = B[(\xi/\overline{\xi})^p - 1]/p \qquad (3)$$

where $p \neq 0$, as in earlier work (Link and Sauer 1999, Link et al. 2006); B and p are parameters determining the effect of effort (described subsequently) and $\overline{\xi}$ is the average value of $\xi_{y,s,i}$. For fixed values of B and ξ, the limiting value of $f(\xi)$ as $p \rightarrow 0$ is $B \log(\xi/\overline{\xi})$, which we take as the defining value for $p = 0$.

The function $F(\xi) = \exp(f(\xi))$ describes the multiplicative effect of effort on counts (Fig. 2): the multiplier is 1 if $\xi = \overline{\xi}$, is an increasing function of ξ if $B > 0$, and decreases to 0 as effort decreases to zero if $p \leq 0$. For $p = 0$, $F(\xi) = (\xi/\overline{\xi})^B$; counts are proportional to effort if $p = 0$ and $B = 1$. Thus the practice of scaling counts by effort (a traditional expedient in analysis of CBC counts; Butcher and McCulloch 1990) is equivalent to assuming $p = 0$ and $B = 1$. If $p = 0$ and $0 < B < 1$, the second derivative of $F(\xi)$ with respect to ξ is negative: there are "diminishing returns" in the number of birds counted as effort increases. Indeed, the same is true for any positive value of B if $p < 0$; in addition, $F(\xi)$ approaches an asymptote at $\exp(-B/p)$.

The model thus allows a reasonable description of the effect of effort, and is sufficiently flexible to allow a formal evaluation of the model implicitly stated when counts are scaled by effort prior to analysis.

Modeling population effects

The quantities $\mu^{\text{CBC}}_{y,s}$ and $\mu^{\text{BBS}}_{y,s}$ are survey-specific indices to population size. It is not to be expected that $\mu^{\text{CBC}}_{y,s} = \mu^{\text{BBS}}_{y,s}$. In the first place, the surveys are conducted at different times of the year. Also, the two surveys produce counts according to entirely different protocols, and consequently at different scales: for the Carolina Wren data considered here, 29% of the BBS counts were zeros, vs. 22% for the CBC; for nonzero counts, the mean ($\pm$SD) for the BBS was 14.0 $\pm$ 14.5, vs. 43.2 $\pm$ 61.2 for the CBC.

Despite these differences, we can describe temporal changes in $\mu^{\text{CBC}}_{y,s}$ and in $\mu^{\text{BBS}}_{y,s}$ using a set of shared parameters. Let $W_{y,s}$ denote the log of the proportional change in population size associated with the winter–spring season of calendar year y in stratum s, and let $S_{y,s}$ denote the log of the proportional change in population size associated with the summer–fall season. Recalling that the CBC is conducted in December, and the BBS in June, we can describe temporal changes in counts over

the surveys' annual cycles as

$$\mu^{CBC}_{y+1,s} = \mu^{CBC}_{y,s} + W_{y+1,s} + S_{y+1,s} \qquad (4)$$

and

$$\mu^{BBS}_{y+1,s} = \mu^{BBS}_{y,s} + S_{y,s} + W_{y+1,s}. \qquad (5)$$

Given that we can estimate $\mu^{CBC}_{y,s}$ and $\mu^{BBS}_{y,s}$, for $y = 1, 2,$ ..., Y, Eqs. 4 and 5 suggest that we can recover information about seasonal components of population change $W_{y,s}$ and $S_{y,s}$.

We accomplish this by a reparameterization of the model in Eq. 2. In the Appendix we demonstrate that the $2Y$ estimable values $\mu^{CBC}_{y,s}$ and $\mu^{BBS}_{y,s}$ ($y = 1, 2, 3, ..., Y$) stand in one-to-one correspondence with an alternate set of $2Y$ quantities, namely, $\mu^{BBS}_{1,s}$, $\mu^{BBS}_{2,s}$, $\mu^{CBC}_{1,s}$, $\delta_{y,s}(S) = S_{y,s} - S_{1,s}$ ($y = 2, 3, ..., Y$), and $\delta_{y,s}(W) = W_{y,s} - W_{2,s}$ ($y = 3, 4, ..., Y$). The two sets of parameters are equivalent in the sense that either set can be calculated from the other. Thus it is possible to estimate the values $\delta_{y,s}(S)$ and $\delta_{y,s}(W)$. These values will be used in a hierarchical model, described next, to examine patterns of variation in seasonal components of population change.

Hierarchical structure

Conventional (nonhierarchical) models treat parameters as either fixed and unrelated quantities, or as deterministically related. Hierarchical models allow examination of weaker, stochastic pattern among parameters. In this section we propose a latent structure of variation among parameters $S_{y,s}$ and $W_{y,s}$ governing seasonal increments in population sizes, and examine its expression in terms of the estimable parameters of our model (Eq. 2).

To ease notation somewhat, we omit subscripts s for strata in this section; nevertheless, all of the parameters described here are stratum specific.

We treat the parameters S_y as independently sampled from a normal distribution, with mean $E(S)$ and variance $\sigma^2(S)$. We also model the winter–spring parameters W_y as independently distributed normal random variables, with variance $\sigma^2(W)$, but we suppose that the mean value of W_y is governed by a linear regression on ψ_y, a stratum-specific index of winter severity to be described subsequently. Thus

$$E(W_y) = \alpha + \beta\psi_y. \qquad (6)$$

We cannot estimate S_y values; hence we cannot estimate $E(S)$. However, given that we can estimate $\delta_y(S) = S_y - S_1$, it is not surprising that we can estimate $\sigma^2(S)$. Similarly, we cannot estimate W_y values; hence we cannot estimate α in Eq. 6. However, the estimability of $\delta_y(W) = W_y - W_2$ leads to estimability of β in Eq. 6 and of the variance $\sigma^2(W)$.

Why are these parameters of interest? Parameter β is of interest per se, as a measure of the effect of the winter severity. The variances $\sigma^2(S)$ and $\sigma^2(W)$ describe the stability of the populations in early and late portions of

the year. Indeed, considering Eqs. 4 and 5, we may decompose the annual change in population size as

$$\log(\text{proportional population change, year } y)$$
$$= (W_y - \beta\psi_y) + \beta\psi_y + S_y. \qquad (7)$$

Eq. 7 is a partitioning into winter–spring effects adjusted for winter severity, effects due to winter severity, and summer–fall effects. The three associated components of variation are $\sigma^2(W)$, $\sigma^2(\psi) = \beta^2\text{Var}(\psi)$, and $\sigma^2(S)$; here $\text{Var}(\psi)$ denotes the (stratum-specific) temporal variation in the winter severity index. Of special interest are the quantities $\sigma^2(\psi)/(\sigma^2(W) + \sigma^2(\psi))$, the proportion of winter variation associated with winter severity, and $(\sigma^2(W) + \sigma^2(\psi))/(\sigma^2(W) + \sigma^2(\psi) + \sigma^2(S))$, the proportion of annual variation attributable to winter effects. These quantities are estimable in our joint analysis of CBC and BBS data, but not from either data set alone.

Priors

The quality of the data varies substantially among strata. Thus, rather than assigning independent non-informative priors to the variances $\sigma^2_s(S)$ (for summer–fall effects), we treated these as being lognormally distributed across strata. The variances $\sigma^2_s(W)$ (for winter–spring effects) were handled similarly. Stratum-specific parameters p_s and B_s, describing the effect of effort in the CBC, were treated as samples from normal distributions, as were the regression parameters β_s for winter severity. We treated the observer/route effects for the BBS as being sampled from a common mean zero normal distribution with variance $\sigma^2(\text{Obs})$; similarly, we treated the circle effects for the CBC as sampled from a common mean zero normal distribution with variance $\sigma^2(\text{Circle})$.

All of the mean parameters for groups of parameters varying across strata were assigned flat priors. All of the precision parameters for groups of parameters varying across strata were assigned gamma priors, $\Gamma(\alpha, \beta)$, parameterized to have mean α/β and variance α/β^2; we set $\alpha = \beta = 0.001$ in all cases. The first-year observer effect in the BBS, η, as well as parameters $\mu^{BBS}_{1,s}$, $\mu^{BBS}_{2,s}$, and $\mu^{CBC}_{1,s}$ were assigned flat priors.

DATA AND ANALYSIS

The intersection of states or provinces with physiographic regions (Bird Conservation Regions [BCR]; Sauer et al. 2003) form convenient strata for analysis of both the BBS and the CBC (Sauer et al. 2003). We identified 70 state/physiographic strata covering the range of the Carolina Wren (Sauer et al. 2005). BBS and CBC data for the 38-year period from 1966 to 2003 consist of 29 732 BBS counts made by 4949 observers and 26 998 CBC counts on 1327 circles.

For two weather stations in each stratum, we obtained data on daily snow coverage from NOAA's National Operational Hydrologic Remote Sensing Center (*avail-*

able online).[2] We defined "snow-cover days" as those on which the average depth at the two stations was at least 4 cm. Our measure of winter severity for the Carolina Wren was the number of snow-cover days in year y, stratum s between 1 January and 31 March, which we denote as $\psi_{y,s}$.

We analyzed the data using Markov chain Monte Carlo, implemented in program WinBUGS (Spiegelhalter et al. 1999). We generated Markov chains of length 60 000, discarding the first 10 000 values as burn-in; this calculation took slightly more than 40 hours on a 3.2-GHz Pentium system.

RESULTS AND DISCUSSION

WinBUGS code, data files, and summaries are available in the Supplement.

Sampling effects

Observer effects in the BBS and effort effects in the CBC are nuisance parameters: they are of little scientific interest per se, except as sources of variation that must be controlled for in order to obtain reliable inference from the data sets. We briefly summarize estimates relating to these nuisance parameters for their interest as descriptors of the surveys.

Variation among BBS observers was substantial, with $\sigma(\text{Obs})$ having a posterior mean of 0.918 (0.013); here and subsequently, numbers enclosed in parentheses are posterior standard deviations, the Bayesian equivalents of standard errors. We conducted an informal analysis of trend in the observer pool, regressing estimated observer effects on the observer's first year of service. The effect was small, both in terms of actual magnitude (0.43%) and in explanatory value ($R^2 = 0.003$), but statistically significant (SE = 0.11%). More importantly, an effect of this magnitude is substantial relative to the rates of population change typically encountered for avian populations.

The first year of service parameter, η, was estimated as -0.021, with 97% of the posterior mass on negative values. Thus the general tendency for BBS observers to count fewer birds than expected in their first year of service is in evidence in the Carolina Wren data.

As anticipated, CBC counts had greater overdispersion than BBS counts: the standard deviations of $\sigma_{\text{CBC}}(\text{Noise})$ and $\sigma_{\text{BBS}}(\text{Noise})$ had posterior means of 0.483 (0.004) and 0.287 (0.003), respectively.

Recall that the effect of effort ξ on CBC counts was modeled by a multiplicative factor governed by parameters B and p (Eq. 3 and subsequent discussion). Preliminary analyses indicated that stratum-specific estimates of p were poorly informed by the data. Using the ratio of posterior variance to prior variance as an index to shrinkage (i.e., as a measure of the uncertainty in estimating individual parameters), we noted that the

median shrinkage across strata was 69%, and that only 13 of 70 estimates had shrinkage less than 50%; estimates (posterior means) ranged from -0.28 to 0.20. We thus decided to assume a common value of p, which was estimated as -0.003, with posterior standard deviation of 0.023. There was therefore no indication that the simpler effort effect model, $F(\xi) = (\xi/\bar{\xi})^B$, corresponding to $p = 0$, is not adequate. Estimates of stratum-specific values of B were well informed by the data: median shrinkage toward the overall mean of 0.879 (± 0.028) was 32%. Posterior means of B ranged from 0.584 to 1.155; 56 of the 70 values were less than 1.00. We may thus summarize the effort effect analysis as indicative of diminishing returns ($0 < B < 1$), but without an apparent asymptote ($p < 0$).

Population effects

The posterior mean values of $(\sigma^2(W) + \sigma^2(\psi))/\sigma^2(W) + \sigma^2(\psi) + \sigma^2(S))$, the proportion of variation in population size associated with winters, ranged from 0.570 to 0.952, with a median value of 0.810 across the 70 strata. Had these posterior means and associated standard deviations been point estimates and standard errors of values sampled from a common normal distribution, the mean and standard deviation of this prior distribution would be estimated as 0.823 (± 0.016) and 0.053 (± 0.016), respectively. Carolina Wrens are nonmigratory and no reproduction occurs during W–S seasons; hence, variation in survival during W–S seasons is the primary source of variation in their populations.

Posterior mean values of $\sigma^2(\psi)/(\sigma^2(W) + \sigma^2(\psi))$, the proportion of winter variation explained by our index to winter severity, ranged from 0 to 0.612; for only 13 of the 70 strata was the value greater than 0.20, and in only 6 of the 70 was the value greater than 0.30. Thus our index of winter severity did not consistently describe a large portion of the winter component of variability. Because the range of the Carolina Wren is primarily centered in the southeastern United States but extends into New England, this wide variation in the explanatory value of winter severity is to be expected. Severe winters are rare in the southern part of the Carolina Wren range, but common at the northern edge of the range; it is not to be expected that winter severity would explain a large portion of the variation in regions where winter mortality is a rare phenomena.

Nevertheless, posterior means of the winter severity regression coefficient β_s were negative for 66 of the 70 strata, with values ranging from -0.032 to 0.001; in 18 cases, the posterior mass below zero exceeded 97.5%. The stratum-specific values were well estimated: the ratio of posterior variance to prior variance (an index of shrinkage) had quartiles of 18%, 29%, and 85% across strata. The posterior mean was -0.0115 (± 0.0022), corresponding to a 1.1% drop in population for each snow-cover day. This result greatly refines the conclusion of Mehlman (1997), providing a quantitative view of the effects of snowfall. Carolina Wrens are well-
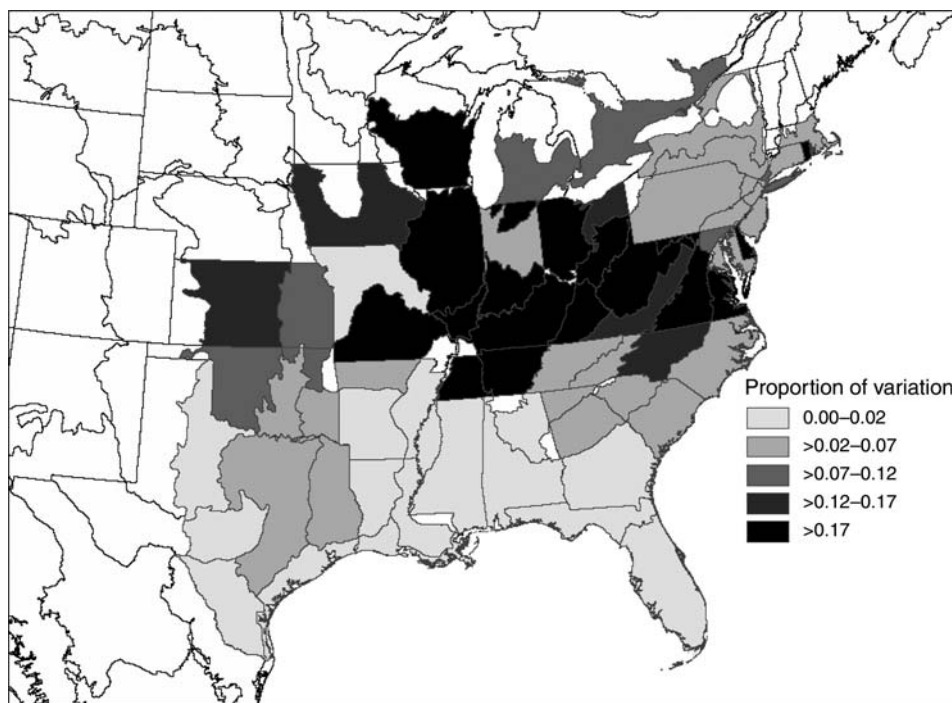
[2] ⟨www.nohrsc.noaa.gov⟩

Fig. 3. Proportion of the winter population variation associated with the snow depth covariate, $\sigma^2(\psi)/[\sigma^2(W) + \sigma^2(\psi)]$. Extreme northern populations of Carolina Wrens are of low abundance, tending to be supporting by feeders during long periods of snow cover; effects of snow cover have been especially evident in the central portion of the range (see e.g., Wetmore 1919).

known to be extremely susceptible to starvation associated with prolonged snow cover (Wetmore 1919), and population declines of more than 50% have been documented in association with severe winters (Sauer et al. 1996). We note that the proportion of winter variability explained by snow depth varies spatially, and is largest in the northern portion of the species' range (Fig. 3).

Conclusions

The novelty of our analysis lies in describing two large-scale surveys by a common set of population parameters, while controlling for sampling effects specific to the individual surveys. For species that are nonmigratory, joint analysis of BBS and CBC data allows us to make inferences not possible from either survey alone. Many important covariates associated with animal population change (e.g., West Nile Virus exposure and severe weather such as hurricanes, droughts, and prolonged snow depth) are seasonal, and our modeling describes an approach that permits use of existing information to better associate seasonal population change with these covariates. We note with interest a reviewer's comment that, for closed populations, the distribution of parameters $W_{y,s}$ describing winter–spring population change on the log scale is probably non-positive, and could possibly be negatively skewed; one could perhaps assume that $-W_{y,s}$ follows a gamma distribution. Our analysis being based on

differences $\delta_{y,s}(W) = W_{y,s} - W_{1,s}$, it seems unlikely that the results will be sensitive to our treatment of $W_{y,s}$ as normally distributed.

The hierarchical structure also permits a variety of options for evaluation of spatial patterns, or alternative models for the effects of covariates. Although our application estimated a similar regression coefficient in each region, elaborations could include placing a conditional autoregressive or other spatial model on the coefficient to permit evaluation of spatial patterns in the relationship. Another possibility, suggested by a reviewer, is the use of a threshold model for the effect of snow depth. This and many other reasonable alternative model formulations could be examined under the new framework.

The hierarchical model facilitates the integration of disparate analyses and provides a natural framework for combined analysis of demographic data and population count data. For example, supplemental information from seasonal count surveys can be integrated in capture–recapture analyses that model components of population growth (e.g., Nichols et al. 2000), providing additional information that can be used to separate demographic features such as immigration and emigration from survival.

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APPENDIX

Reparameterization of the model (*Ecological Archives* E088-002-A1).

SUPPLEMENT

WinBUGS files and notes (*Ecological Archives* E088-002-S1).

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